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THE BIOLOGY OF XYLOPHILIC CECIDOMYIIDAE (DIPTERA)

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Abstract.—The general biology of six new Nearctic species of wood vessel-inhabiting Cecidomyiidae is described. Adults have fixed activity periods which vary with species. Females oviposit in exposed, non-decayed hardwood vessels. Host wood becomes progressively less attractive for oviposition as fungal growth on exposed surfaces increases. In all species larval development requires a minimum of 14 days, but emergence from the vessel may be delayed for several weeks. Emergence requires rainfall sufficient to saturate the wood. Pupation takes place in the ground and the length of the period varies with species and sex; the minimum time between generations is 24 days. The insects overwinter either as larvae in the vessels or as larvae in cocoons in the soil. Sex ratios in two species are 3:1 and 4:1 respectively with a predominance of females. Larvae are parasitized by platygasterid wasps; the parasitism rate is approximately 5%. Ovipositing female midges are preyed upon by empid flies. Techniques for rearing the midges in the laboratory are described.

Larvae of the family Cecidomyiidae have a great diversity of feeding habits. Most attack the meristematic tissues of a wide variety of plants such as hard and soft wood trees, root crops, grains, and fruits, and many are of economic importance. In some species the larvae are zoophagous, attacking small prey such as aphids, scale insects, and mites. Others feed on decaying vegetation and some are mycophagous.

Amidst this diversity there occurs a unique group of xylophilic larvae that live in the xylem vessels of freshly cut hardwoods. The adult females seek out newly felled logs and broken branches and oviposit into the exposed vessel openings. Kieffer (1900, 1913) described several species of xylophilic cecidomyiids and outlined the main events in the life cycle of some European species, but no significant contributions to the biology of this group have been published subsequently. We are reporting the general biology of species of xylophilic Cecidomyiidae found during a period of study in northeast Ohio. The study involved the collection and identification of xylophilic species and observations on the general life cycle.

MATERIALS AND METHODS

Field and laboratory observations were made on larvae and adults collected from local populations. *Quercus alba* L. (Fagaceae) and *Fraxinus americana* L.

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(Oleaceae) were used early in the study as suitable hosts. Initially all wood samples were at least 12.5 cm in diameter and 30 cm long. As the study progressed, branches of varying sizes and additional species of hardwood including *Juglans nigra* L. (Juglandaceae), *Ulmus americana* L. (Ulmaceae), *Carya ovata* (Mill.) K. Koch (Juglandaceae) and *Sassafras albidum* (Nutt.) Nees (Lauraceae) were tested for host suitability.

Two field sites chosen were a tree-line on the edge of an open field in Canal Fulton, Ohio and a heavily wooded yard in Akron, Ohio. In both of these areas the wood samples were well shaded, which prevented rapid desiccation of the logs. Field study dates for 1981 were from June 3 to November 15. In 1982, observations began on May 15 and continued through December 7 as the weather was unseasonably warm.

Wood samples were observed for insect activity and records were kept of oviposition and subsequent larval emergence. Emerging larvae were collected by placing the wood samples in large rectangular plastic bins. Once a connection between rainfall and larval emergence was established, water was added to the bins to stimulate the emergence of mature larvae. The larvae were then collected from the water in the bins with Pasteur pipettes. All larvae, adults and parasitic wasps for taxonomic identification were preserved in 70% ethanol.

A system was designed for laboratory rearing of adult midges from collected larvae. Several inches of sterile potting soil were packed into 10 cm diameter plastic plant pots and covered with 5 cm of loose soil (Peterson, 1964). The collected larvae were counted and added to the surface of the dampened soil; no more than 300 larvae were placed in a single pot. As cecidomyiid larvae can spring a distance of several centimeters (Richards and Davies, 1977), a 10 cm glass Petri dish lid was placed over each pot to prevent escape. The pots were held indoors at room temperature and sprayed with water as needed to prevent dessication. After pupation the Petri dish lid was removed and replaced with an inverted 10 cm plastic funnel with nylon mesh covering the stem opening. This facilitated collection of the emerging adults. All pots were examined daily for the presence of adult midges and the length of the pupation period was recorded for both sexes. Eclosion time was noted for each species.

New adults were placed in cages constructed from glass aquaria with tightly fitting nylon mesh coverings. One pot was placed in each 30 cm × 50 cm × 25 cm cage. A 5% sugar solution in small glass vials with cotton wicks (Peterson, 1964) was kept in the cages as a food source for the adults. Humidity was maintained by misting the sides of the cages. The cages were held in rooms at ambient temperature (15–30°C) and kept from direct sunlight. All pots were held for several weeks past midge ecolsion in order to collect and record the emergence of any parasitic wasps.

Results and Discussion

Taxonomy

Adult and larval gall midge identifications were made by Raymond J. Gagné, Systematic Entomology Laboratory, IIBIII, USDA, Washington, D.C. Six new species in one new and three extant genera were represented and are described as *Trogodiplosis flexuosa, Xylodiplosis longistylus, Ledomyia emilyae, Ledomyia mira, Ledomyia parva,* and *Trichopteromyia denticauda* in Gagné (1985).

Life Cycles

We observed that larvae overwinter either in the soil or in the vessels of the hardwood hosts. Unseasonably high temperatures in December and January may thaw the ground and temperatures of 21°C or higher may enable the larvae to leave their above-ground location in the wood and enter the soil. Here they spin loose silken cocoons; they do not pupate, but remain in the larval form. In northeast Ohio, pupation occurs about the end of April and the adults begin to emerge in mid-May. Our studies confirm Barnes's (1946) observations that gall midge adults emerge at fixed periods in the day. Adults of *X. longistylus* and *T. flexuosa* emerge from the soil in late afternoon and *Ledomyia* spp. and *T. denticauda* emerge during the morning hours (Table 1).

Males generally emerged two to three days before females and consequently a population of new adults consists mostly of males. The average adult life lasts 3 to 5 days, but under laboratory conditions some females lived as long as 9 days. Although in some cecidomyiids the sex ratio is 1:1, there is a predominance of females in many species. Mamaev (1968) cites an average ratio of 35:65 of males to females in many phytophagous species; we have observed ratios as high as 1:4 in xylophilic species. The sex ratios listed in Table 1 are based on the percentages of all adults collected from the caged populations.

Although we have observed mating in caged populations we have not seen it under field conditions. Kieffer (1900), however, noted that mating occurs on the ground almost immediately after the females emerge, even before the females are able to fly. After coupling, only females leave the eclosion site to search for freshly cut hardwood; thus the males are not attracted to the oviposition site. Kieffer suspected this and we have confirmed it in field and laboratory observations.

The females of each genus have a fixed activity period for oviposition (Table 1). *Ledomyia* spp. and *T. denticauda* oviposit throughout most of the afternoon; *X. longistylus* and *T. flexuosa* are nocturnal, with some *Trogodiplosis* females ovipositing as late as 5 A.M. There is very limited movement outside of these oviposition periods, the adults often remaining quiescent for many hours.

When approaching a suitable host, the females use a flight pattern adopted by many female insects in the location of oviposition sites (Dethier, 1947). Initially, flight is apparently random, but when the females are within several centimeters of the wood surface their flight takes a straight-line pattern to the edge of the log and they alight. The search for a vessel suitable for oviposition begins immediately; the end of the abdomen is deflexed and the tip of the ovipositor is applied with obvious pressure to the wood surface. While the female walks in an apparently random pattern (even walking backwards), the tip of the ovipositor is in constant contact with the surface. The end of each vessel is probed with the tip of the ovipositor; eventually a suitable vessel is located, the abdomen lowered and the ovipositor extended into the vessel. Although the search appears random and may take several minutes, the female always limits her search to the outer edges of the xylem (sapwood vessels).

Once oviposition has been initiated, the female is not easily disturbed. During normal resting periods, however, females are easily agitated by such factors as vibrations, abrupt changes in light intensity, or contact with other individuals. Barnes (1951) noted that females of *Xyboliplosis praecox* Winnertz oviposit "so intently that they can easily be picked up with the fingers." We have noted that

Table 1. Life cycle data of six species of xylophilic cecidomyiids encountered during this study.

Cycle	*Xylodiplosis longistylus*	*Trogodiplosis flexuosa*	*Ledomyia* spp	*Trichopteromyia denticauda*
Eclosion period	3 PM to 5 PM	3 PM to 5 PM	8 AM to 10 AM	8 AM to 10 AM
Oviposition period	8 PM to 11 PM	12 AM to 5:30 AM	1 PM to 5 PM	2 PM to 6 PM
Minimum length of larval stage	14 days	14 days	14 days	14 days
Length of pupal stage:				
Male	14 to 16 days	10 to 12 days	14 to 16 days	<14*
Female	15 to 17 days	12 to 14 days	15 to 17 days	>20*
Sex ratio: male : female	1:3	1:4	*	*

* Insufficient data.

neither bright microscope lamps or contact with other searching females interrupts oviposition.

Sometimes, even when the vessel appears to be of suitable diameter, the ovipositor is withdrawn immediately and searching resumed. Possibly the vessel is rejected because of some obstruction below the surface or because it already contains an egg. Although we have no direct evidence that a female will not oviposit in an already occupied vessel, we have never observed more than one larva emerging from a vessel.

We were unable to follow early developmental stages in the vessels partly because of problems in recovering undamaged eggs or larvae from the woody tissue. However, the duration of the larval stage was determined for all the genera studied (Table 1). In all the species, the mature larvae begin to emerge from the vessels 14 days after oviposition if conditions for emergence are favorable.

We have confirmed Kieffer's (1913) observation that rainfall is an essential factor in creating the conditions that are favorable for larval emergence. During a summer with frequent rainfall the larvae emerge on a steady basis and several generations are possible. If several days elapse between rainfalls, the surface of the wood dries and the larvae remain in the vessels until the next hard rain. Kieffer (1913) suggested that the moisture is needed to soften the wood, thus easing the escape of the larvae from the vessels. However, we observed no change in vessel diameter when dry wood samples (wood held in the laboratory for 2 weeks) were soaked in water for several hours. Barnes (1946, 1956) noted that moisture is essential to the survival of mature emerged larvae of several genera of cecidomyiids and we observed that emerged xylophilic larvae are very susceptible to dessication unless promptly given a moist medium in which to pupate. Therefore, rain appears to act as a sign stimulus for the release of emergence behavior; when the larvae react to this stimulus they are more likely to encounter moist soil in which to pupate.

Once the larvae leave the vessels, moisture is essential. As long as they remain in the wood they can withstand extended periods of drought. Kieffer (1900) noted that during a dry spell larvae of *X. praecox* remained in the vessels for one month past maturity. We have held *U. americana* logs (10 cm diameter × 60 cm long) inhabited by xylophilous larvae in the laboratory for 60 days at 20 to 22°C and approximately 55% humidity, during which time no larvae emerged from the logs. At the end of this period the logs were placed in bins of water and within 3 hours the larvae began to emerge.

Once free of the vessel, the larvae either fall to the ground directly or spring from the log. Once on the soil, the larvae immediately begin digging but do not penetrate more than 5 cm deep. The vast majority of the larvae then spin a silken cocoon.

Larval Food

Many cecidomyiid larvae that develop in wood are mycophagous and are typically found in wood with obvious decay. Kieffer (1900) expressed surprise after observing cecidomyiid larvae emerging from oak logs which had no trace of decomposition; we have confirmed this observation. Although we have not identified the source of the larval food, the following observations are pertinent. *Xylodiplosis* shows some relationship to *Contarinia*, a large genus of primarily

plant feeders (see Gagné, 1985), but the other xylophilic larvae encountered during this study belong to groups that are mycophagous. Nijveldt (1969) and Batra and Batra (1967) have suggested that some cecidomyiid females supply fungal spores to the developing larvae. It is possible that the larvae feed on inconspicuous yeast or molds in the vessels, but we have not been able to detect such fungi by light microscopy. We have observed, however, that in damp weather fungi develop within a few weeks over the cut surface of the logs and such logs yield fewer larvae. Originally we suspected that this was due to competition for food between the developing larvae and the established fungi. However, experiments on host selection (ms in preparation) indicate that there is a progressive loss of oviposition site-attractiveness in the presence of fungi.

Parasites and Predators

Larvae of most Platygasteridae (Hymenoptera) parasitize cecidomyiid larvae, and several species have been reported from xylophilic larvae. We observed females of several species of *Synopeas* and *Leptacis* ovipositing in vessels previously visited by female cecidomyiids. Development of the parasite larvae is suppressed until the host larvae leave the wood and pupate. The parasites then develop rapidly and begin to emerge 14 days after the nonparasitized adult midges emerge. An overall parasitism of approximately 5% was observed.

While remaining in the vessels, the xylophilic larvae are relatively safe from predators. However, both Kieffer (1900) and Huggert (1980) noted that after emergence many larvae became trapped in spider webs below the stacked logs. Huggert described the larvae and pupae being attacked by a cimicoid bug, *Loricula elegantula* (Bär). Several times we observed a dance fly (Empididae: Diptera) preying upon ovipositing midges. The fly concealed itself in the edge of the bark, quickly ran onto the cut surface of the log, captured the female midge, and returned with its prey to a crevice in the bark. The activity period of the dance fly appeared to correspond with the peak activity period of the diurnal midges.

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